EXHIBIT 5
A89 – A113

SPECIALTY CORNS

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CRC Press
Boca Raton Ann Arbor London Tokyo

Library of Congress Cataloging-in-Publication Data

Specialty corns/editor, Arnel R. Hallauer.
p. cm.
Includes bibliographical references and index.
ISBN 0-8493-4612-6
1. Corn—Varieties. 2. Corn—Breeding. 3. Corn—Germplasm resources. 4. Corn—Utilization. I. Hallauer. Arnel R., 1932–
SB191.M2S6252 1993
633.1 523—dc20 93-25364
CIP

No claim to original U.S. Government works
International Standard Book Number 0-8493-4612-6
Library of Congress Card Number 93-25364
Printed in the United States of America 1 2 3 4 5 6 7 8 9 0
Printed on acid-free paper

Chapter 3

HIGH AMYLOSE AND WAXY CORNS

Virgil Fergason

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0-8493-4612-6/94/$0.00 + $.50

I. INTRODUCTION

Ever since the discovery of its existence in North American, corn (*Zea mays* L.) has had a prominent role in the development of American agriculture. Somewhere in its history lies the secrete for its extreme genetic diversity. This variability has made it possible over the past several decades to develop a multitude of unique varieties and hybrids, each of which has its own distinctive chemical and physical properties. Perhaps the most important factor for its continued persistence in our society is the capacity for corn to produce large quantities of desirable carbohydrates over a wide geographical area and its adaptation to an array of soil types, climatic conditions, and cultural practices.

II. STARCH: ITS ISOLATION, SEPARATION, AND IDENTIFICATION

Starch is the major storage carbohydrate within the plant kingdom and is found in all organs of most plant species. In excess of 95% of the commercial starch produced in the U.S. is from corn.[1] The corn endosperm consisting of approximately 87% starch is the major starch storage component of the corn kernel, and it comprises nearly 82% of the total grain weight.[2] Simple as it may seem, starch is actually a complex arrangement of carbohydrate components arranged in a variety of forms within individual starch granules.[1,3] Starch has been defined as a polymeric carbohydrate consisting of anhydroglucose units linked together primarily through α-D-(1→4) glucosidic bonds. Normal dent or the commonly grown corn in the U.S. possesses two types of polymers—amylose and amylopectin (Figures 1 and 2). They are present in corn endosperm in an approximate ratio of three parts amylopectin to one part amylose. Amylose may contain from 200 to 2000 or more anhydroglucose units linked together in a linear order by α-D-(1→4) glucosidic bonds. Amylopectin is a higher molecular weight polymer having anhydroglucose units linked together as in amylose by the α-D-(1→4) bonds, plus periodic side branches of anhydroglucose units connected at the carbon 6 position by α-D-(1→6) glucosidic bonds. Additional research has shown other polymers with some side branching occurring by α-D-(1→3) glucosidic bonding.[4] Starch consists not only of the normal amylose and amylopectin fractions but also of intermediates between these two polymers. These fractions may be amylopectin-like structures with a reduced degree of branching, or there may be side branches having a longer linear chain of anhydroglucose units. In addition, there are amylose types having a small degree of shorter side branches. All of these ramifications of starch types add to the difficulty in understanding the starch granule, its chemical and physical architecture, and the synthesis and deposition of starch in various plant organs. To gain a better understanding of the starch complex, the starch component must be isolated from plant tissue without causing modification of its physical and chemical properties. Whistler and Daniel,[5] and Young,[3] presented reviews of "starch fractionation", a procedure for the separation of amylose and amylopectin types. Once isolated, there are reliable methods for identification of these two starch polymers which are distinct in their ability to form iodine-starch complexes when treated with a dilute iodine solution.[6,7] Amylose readily forms an insoluble complex with iodine, as opposed to amylopectin, which has a reduced affinity for iodine absorption; consequently, differential color strains are expressed. Iodine-stained amylose expresses a deep blue color while an amylopectin iodine complex results in a reddish-brown color. These colors are not absolute because the starch molecules themselves may be nonhomogeneous, thereby leading to differential staining. Length and number of side branches or length of the linear fraction affect the iodine starch complex and iodine absorbency thus resulting in different color reactions. No attempt will be made in this chapter to elucidate on starch fractionization procedures or

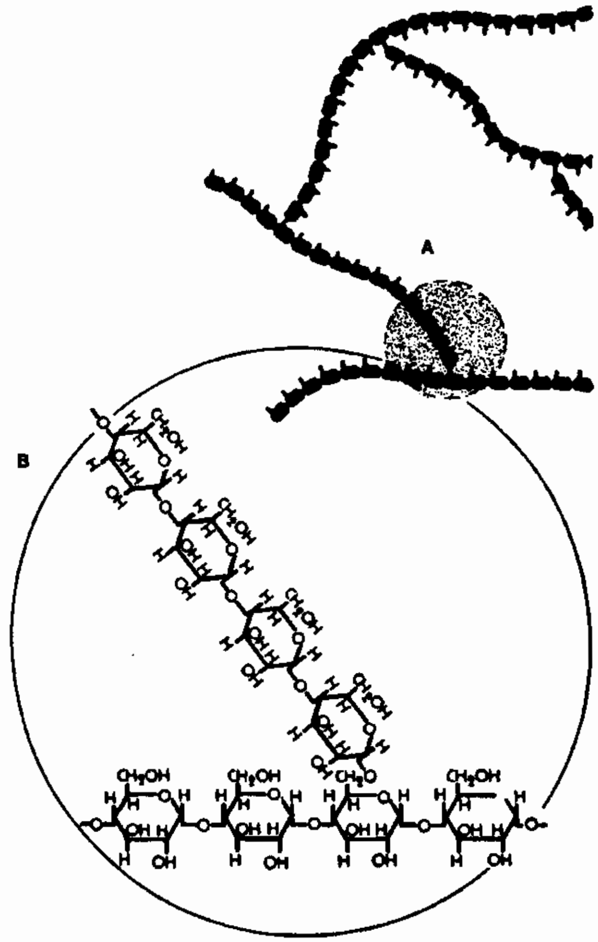

FIGURE 1. (A) Diagram of a fragment of a branched-chain molecule of the amylopectin fraction of starch. (B) Enlarged view of shaded section of diagram showing chemical structure and linkages at point of branching. (Paper presented by F. R. Senti before the 23rd National Farm Chemurgic Conference, Chicago, April 23, 1958.)

the impact they have had on starch utilization. The progress made today in the starch industry would not have been possible without the wealth of information gained from the study of these two starch components whose isolation, separation, and identification were essential.

It seems appropriate at this time to pose the questions: "Why is it necessary to determine the amylose-amylopectin ratio of plant starches and the unique and distinct properties of the starch complex in various plant species and in corn in particular?" Since the beginning of the starch industry, thousands of uses for corn starch have been discovered. These uses require specific starches or combinations of modified starch types. It is therefore imperative that the raw product be made available in the quantity and quality desired. Without adequate procedures for isolation, separation, and identifying these starch components, utilization objectives could not be achieved. Research involving a wide array of corn germplasm has led to the discovery of an enormous degree of variation in their carbohydrate complex. For example, there are corn germplasm sources available that range from less than 20 to 100% complement of amylopectin.

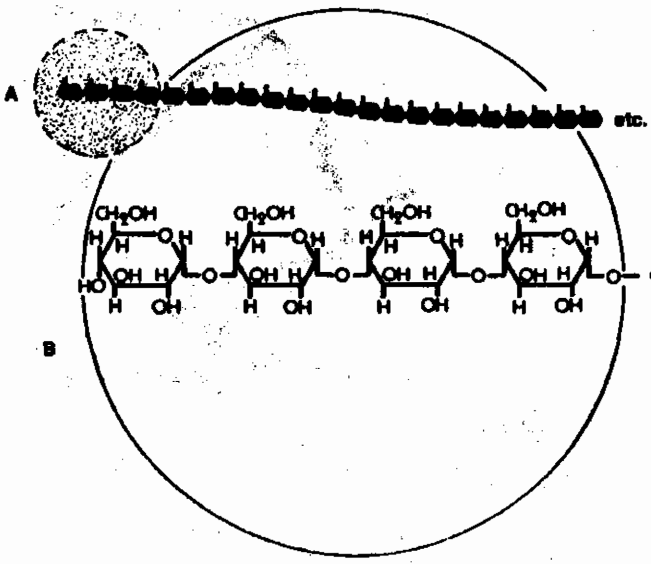

FIGURE 2. (A) Diagram of a fragment of a straight-chain or linear molecule of the amylose fraction of starch. (B) Enlarged view of shaded section of diagram showing chemical structure and linkages. (Paper presented by F. R. Senti before the 23rd National Farm Chemurgic Conference, Chicago, April 23, 1958).

Various methods have been used to determine amylose-amylopectin ratios.[7-17] Potentiometric iodine titrations and spectrophometeric analyses have been used extensively to determine amylose-amylopectin ratios of various starches. The latter method is based on the absorbency of the starch-iodine complex (also called blue-value procedure) and on relating the degree of absorbency to known amylose and amylopectin standards. The potentiometric method is based on the amount of iodine bound by 100 mg of starch and compared to the amount bound by a purified amylose standard. A review of these methods by Shannon and Garwood[7] points out that the amylose estimated by these procedures should be considered "apparent amylose" because the occurrence of branched chain components with long external chains can result in an overestimation of amylose. They also suggested that the presence of short-chain-length amylose components would result in an underestimation of the amylose component. Other investigations have shown similar variations in the architecture of the starch granules.[18-20] From the voluminous amount of research data available, it can be concluded that cornstarches cannot be precisely divided into amylose and amylopectin fractions, but they all blend together through various intermediates of various molecular sizes and weights.

It is obvious that the biosynthesis of starch and its deposition in the corn kernel is very complex and that there is an enormous amount of data available on starch synthesis. For example, by 1963, Sandstedt[21] reported that one volume on carbohydrate chemistry listed more than a thousand references. There are recent reviews which include the latest theories on starch biosynthesis and the enzymes involved in amylose and amylopectin synthesis.[13,17,19,22-34]

It is not the intent of this author to elaborate on starch synthesis in this chapter but rather to present a brief historical background in the development of high amylose and waxy corn and their significance as specialty type corns of today. Specialty corn is a common but somewhat vague description of corn which could be more clearly identified based on its chemical and physical characteristics and by its distinctive nutritional or industrial properties.

Several corn endosperm mutations have been identified that modify both the quality and quantity of carbohydrates in the corn kernel. Many of these mutations are included in other chapters in this publication; therefore, this chapter will be devoted to only the high amylose and waxy corns and the specific mutations responsible for these special types. Since high amylose and waxy specialties differ so dramatically in many properties and have varied and different feed, food, nutritional, and industrial applications, they will be discussed in separate sections.

III. HIGH AMYLOSE CORN

A. INTRODUCTION

The terms "amylose" and "amylopectin" were used about 50 years ago to describe the straight-chain and branched-chain components of starch.[35] Previously, very little was known about the structure or identity of these starch components. In 1942, Shock[36] reported on the isolation of pure amylose and amylopectin starches. Common commercial starches used until then were actually a mixture of amylose and amylopectin. Then in 1943, Bates et al.[9] reported on a new analytical method for estimating the amylose content of plant starches. The results from these early investigations kindled renewed research interest into the use of these unique starch components in the starch industry. Subsequent discoveries and advancements in starch fractionation procedures provided more incentives for expanding the use of these purified starch fractions in various food and industrial applications. However, the fractionation of normal starch to obtain higher levels of amylose starch is very costly. Likewise, this method provides large quantities of amylopectin starch which can be obtained more economically from waxy corn, which is discussed later in this chapter.

Various projects were initiated by several research scientists in an attempt to find plant sources having naturally enriched levels of amylose starch production. Subsequently, amylose analyses were made on a large array of various cultivated plant species including peas, barley, wheat, rice, sorghum, potatoes, and corn.[3] Results from these investigations included reports of corn endosperm mutations having higher than normal amylose contents.[4,7,23,37] Dunn et al.[38] reported an amylose content of 77% from a triple recessive isolation of *du su su2*; however, the total starch content of this triple recessive mutant combination was reduced substantially. In addition to these studies involving endosperm mutations, surveys were made among many domestic and foreign sources of corn germplasm to find higher levels of amylose synthesis. In 39 different Indian corns from North, Central, and South American, amylose values were found to range from 22.2 to 28.3% with averages at the normal level of nearly 27% amylose.[39] Deatherage et al.,[40] in a survey of 200 domestic inbreds and varieties including more than 75 foreign varieties, reported amylose values ranging from 0 to 36%. The first real breakthrough in obtaining higher amylose starch levels without corresponding significantly lower total starch production came in 1952 with the discovery of the *ae* gene located on Chromosome 5.[41] Other mutants at the *Ae* locus have subsequently been reported.[42] These alleles, when compared to the original *ae* mutant, were found to be associated with slight modifications in amylose-amylopectin ratios as well as some alleles having starches with small amounts of a short-chain type amylose.

Phenotypically, the presence of *ae* can be identified very easily in most germplasm sources by the expression of a tarnished endosperm characteristic.[43] In some genetic backgrounds there may also be varying levels of wrinkling of the pericarp. This wrinkling phenomenon is probably associated with a reduction of sugar conversion to starch, subsequently resulting in a partial collapse of the endosperm. Immediately following the discovery of this amylose-enriching recessive gene, breeding programs in both the private and public sectors were started with objectives to develop hybrids having commercially desirable ag-

ronomic qualities and high amylose starch production. "Amylomaize" was proposed as the name for this new high amylose specialty corn.[44]

B. BREEDING HIGH AMYLOSE CORN

Early in the history of amylomaize, essentially nothing was known pertaining to the inheritance of *ae* and its epistatic interaction with other starch regulating genes. Subsequent work with *ae* and its interaction with other endosperm starch mutations revealed extensive variations in the level of amylose synthesis.[23,41,43,45] Vineyard et al.[46] reported amylose contents ranging from 36.5 to 64.9% from crosses between 135 different inbreds and a common *ae* source. Independent researchers suggested that "modifier genes" from different germplasm were interacting with the *ae* gene to produce various levels of amylose.[43,46] Later work involving amylose synthesis associated with several mutant alleles at the *ae* locus found endosperm starch having from 56.6 to 64.5% amylose.[42] Those differences were attributable to the epistatic effect of the major *ae* allele and its modifiers, thus supporting the theory that a range in amylose values of this magnitude is attributable to the effects of an unknown number of modifiers, interacting with the recessive *ae* gene. Phenotypic expressions may vary among inbred lines converted to high amylose starch production.[41] Fullness of kernel, which is a result of reduced starch production, is the most obvious variant and may continue to be of greatest concern to the breeder because total starch deposition within the endosperm is a major component of grain yield. Early studies of amylomaize revealed that high amylose starch granules differ significantly from those in normal dent corn.[20,47,48] No theories have been proposed to this date to explain why the presence of irregular shaped starch granules increases as the level of amylose synthesis increases. Other studies have shown a decrease in typical angular granules of normal corn with a corresponding increase in very irregular sausage-shaped granules as amylose synthesis increases.[18,20,21,37,49–51]

The primary objective of any corn breeding program should be the development of agronomically superior hybrids with reliable high performance standards over a wide array of growing conditions. In the early 1950s, Bear Hybrid Corn Company, with support from the National Starch and Chemical Company, began an extensive breeding program to incorporate the *ae* gene into agronomically desirable inbred lines and broad-based germplasm sources. It is not possible to phenotypically determine differences in levels of amylose starch production within the homozygous *ae* background. Therefore, the success of a high amylose breeding program is partially dependent upon chemical starch analyses to determine the relative levels of amylose starch syntheses within selected samples from various breeding populations. The Northern Utilization Research and Development Division Laboratory of the U.S. Department of Agriculture at Peoria, IL, performed this analytical service for selected private and public breeding programs until the early 1960s.

The accuracy of amylose determinations is of utmost importance because it is essential in amylose breeding programs to select for very small inherent differences in amylose values; therefore, the error in determination should not exceed the selection differential if breeding progress is to be expected. Consequently, specially designed studies within various amylose breeding programs have provided information which has added to the knowledge needed to enhance the effectiveness of amylose breeding. Consistent progress in increasing the inherent amylose content of corn is dependent upon the successful separation of variations in amylose synthesis induced by genetic vs. environmental influences. Differences in amylose content of varying magnitude have been associated with many factors which include genetic effects as well as environmental influences. Fergason et al.[52] were among the first to provide evidence of kernel position effects on amylose content between ear zones and to demonstrate the occurrence of unequal distribution of amylose within the corn endosperm. Amylose analyses of samples taken from separate ear zones of high amylose inbred lines revealed

amylose contents of 71.9, 69.8, and 67.4% for the base, middle, and tip ear zones, respectively. Similar trends, although of a smaller magnitude, were indicated when amylose analyses were performed on samples taken from different ear zones of four high-amylose hybrids. Highly significant differences in amylose content between endosperm portions were also found. These data revealed average differences as great as 4.8% amylose among starch samples taken from the middle, tip, and crown endosperm portions. Even though this represents a limited number of samples from only a few germplasm sources, it does provide consistent evidence that proper sampling procedures and analytical techniques are very important in any amylose breeding program. These data reflect trends similar to those reported by Boyer et al.,[30] in which they found that an increased amylose percentage was correlated with the physiological age of cells and that larger granules contained a higher amylose percentage. They reported that the basal endosperm cells begin starch biosynthesis late in kernel development and contain small granules with low amylose values.

Considerable evidence exists that environmental effects and cultural conditions can affect the chemical composition of corn grain.[53-58] Initially, Fergason and Zuber[59] reported on the environmental effects on the amylose starch level of six inbred lines grown in eight different states for a period of three years. The six inbreds in their study included one normal dent, four inbred lines which were homozygous for the *ae* gene, and one inbred homozygous for the *dull* (*du*) gene. Small, but highly significant differences were found for both location and year effects, but the differences in amylose content associated with location effects were greater than the difference associated with year effects (5.4 vs. 1.8%). Amylose differences attributable to locations, years, and all interactions were statistically highly significant, thereby supporting the theory that high amylose starch synthesis is associated with complex genotypic- environmental interactions. Correlation coefficients of −0.81 between amylose and degree days, and between amylose and average temperature during the growing seasons suggest that temperatures may have a significant impact on amylose starch synthesis.[59]

Would similar results be expected from environmental effects upon high amylose hybrids? T answer this question, four high amylose single-cross hybrids were grown at 12 locations in 1960 and 1961.[60] Again, highly significant differences in amylose synthesis occurred among entries, locations, and years with the greatest average differences of 7.8% amylose attributable to location effects. Likewise, correlation coefficients of −0.73 between average amylose content vs. degree days for each of the 2 years indicated that cooler temperatures during the growing season resulted in the highest amylose content.

Among other external factors that could influence amylose synthesis is a reduction of photosynthetic leaf area of the plant resulting from hail, leaf diseases, and insect feeding. Loss of leaf area as a result of any of these conditions would have to be considered by the high amylose corn breeder in interpretation of results or before making selections to be included in subsequent breeding populations. Results from a study on the effect of leaf removal on amylose contents of corn endosperm did reveal an association between a reduction in leaf area and lower amylose content of endosperm tissue.[61] The magnitude of these differences was greater among inbred lines compared with differences noted among hybrids (2.5 vs. 0.75%). As expected, the impact on reduced amylose deposition in the endosperm was more pronounced by removing six top leaves when compared with the removal of six bottom or six alternate leaves. Additional studies reported by Helm et al.,[62] which were designed to determine the effect of planting date on high amylose hybrid performance, revealed that delayed planting was associated with increased amylose levels and lower grain yields. Their data indicated an inverse relationship of amylose content and accumulative degree days. They concluded that late planting may be advantageous for maximum amylose content but only with a sacrifice of lower grain yields and reduced performance for other agronomic characteristics.

Nearly 10 years after the discovery of the *ae* gene, the first commercial production and subsequent wet milling of high amylose corn grain occurred. This grain contained an amylose content in the mid 50% range. However, there was immediate interest in obtaining corn grain having 70% or more amylose for use in the starch industry. Continued and increased emphasis has been placed on breeders to develop agronomically superior high amylose hybrids possessing even higher concentrations of amylose starch. Corn breeders have continued to search for new breeding techniques or tools to enhance the effectiveness of their high amylose breeding programs. Perhaps, differential levels of amylose concentrations within corn pollen could provide some assistance to the breeders for selection within their breeding populations. However, unlike the occurrence of low amylopectin starch content from waxy pollen, there is no correlation in amylose content between the pollen and endosperm of high amylose grain.[46,48,63]

The requirements in a high amylose breeding program are broader in scope than in most other programs. It is necessary to consider not only all the usual agronomic requirements of normal dent corn breeding programs but also the level of amylose desired for commercial utilization. The effectiveness of a high amylose breeding program, as in any other, is dependent upon the type and level of genetic variability present in the available breeding populations, and the ability of the breeder to select for the most desirable combinations of the genetic factors involved. Within an amylose breeding program, progress in the development of high amylose hybrids must also emphasize the incorporation of suitable genetic modifiers of the amylose extender gene. Based on prior knowledge of the genetics involved in high amylose starch synthesis, breeders can be confident that the differences between various levels of amylose in breeding selections homozygous for *ae* must be attributable to the accumulation of specific modifiers of *ae*. Presumably more modifiers are required to reach the 75% level of amylose synthesis than to obtain the 65% level or lower. Prior research pertaining to gene dosage effects at the *ae* locus on amylose content of corn endosperm indicated a partial dominance of the wild type *Ae*.[64] It was determined, however, that all genotypes must be homozygous at the *ae* locus so that selection for the accumulation of *ae* modifiers can be achieved.

Earlier research indicated that a significant amount of additive gene action was involved in the inheritance of amylose starch synthesis.[65] When the breeding of high amylose hybrids was still in its infancy, the belief existed among some breeders that the development of amylomaize hybrids would be a simple matter of backcrossing the amylose-producing genes into inbred lines and then combining these lines in various hybrid combinations.[45] They also emphasized that "not only does the recurrent parent background affect the amylose content, but it also affects the phenotypic expression of the kernels". Some dent inbreds that were converted to amylose types produced completely full kernels while others revealed varying levels of collapsing of the crown portions of the kernel, and some gave translucent kernel phenotypes as opposed to the more opaque normal types. In some germplasm sources there were varied frequencies of complete collapse of the endosperm. Presumably in these types, there is little or not starch conversion. This phenomenon increases the difficulty in choosing which normal dent inbreds to convert to high amylose production.

Breeding procedures have been proposed for the development of agronomically adapted amylomaize hybrids.[45,66] These procedures included an alternate backcrossing and selfing sequence for the development of high amylose inbred lines. A minimum of three cycles of backcrossing was proposed. This proposal has serious limitations, especially if the high amylose nonrecurrent parent has undesirable agronomic regulating genes linked to *ae*; therefore, several backcrosses might be necessary to break the linkages and, subsequently, select against these linkages. In addition, unless the recurrent parent possesses the necessary modifiers for the desired level of amylose syntheses, the backcross procedure may have

limitations for achieving the objectives set forth. If only the nonrecurrent parent possesses the modifiers necessary to achieve a specific level of amylose synthesis, then the size of the breeding population becomes a very important limiting factor. Large populations would, therefore, be required to be more assured of obtaining the necessary combination of genes in the selfing generation before making the next backcross. However, if the modifiers are supplied primarily by the recurrent parent, then it becomes much easier to select for the desired level of amylose syntheses. There is no clear answer to the question of how many generations of backcrossing will be required to obtain converted high amylose inbreds. Pleiotropic responses will definitely affect this answer. Some inbreds can be more readily converted to higher levels of amylose production than others, and some inbreds are not conducive to the conversion program. However, the backcross procedures was relatively successful in some of the earlier high amylose breeding programs.

Other amylose breeding procedures have also been very successful in the development of high amylose inbreds and their subsequent hybrid combinations. The relative short duration of hybrid longevity in today's agriculture places added pressure on corn breeders to develop new and improved hybrids as fast as possible. A backcross procedure in a high amylose breeding program has limitations in meeting the demands for the rapid development time of new amylose hybrids. This implies that the use of backcross conversion of the best dent lines should not be the only breeding procedure of a high amylose breeding program. Therefore, alternative breeding methods have been used to enhance the effectiveness of these amylose programs.

Pedigree selection has become a very reliable breeding method in development of new amylose hybrids. As expected, difficulties in utilizing this method are compounded as the degree of dissimilarities between parent breeding populations are increased. Pedigree selection does, however, offer the breeder flexibility in choosing among several options for meeting breeding objectives. It is not the intent of the author of this chapter to elaborate on the actual procedures or the germplasm sources that have been most applicable to the development of inbreds presently being used in commercially available high amylose hybrids. It should be emphasized, however, that the number and size of kernel samples selected for amylose starch analysis within a breeding population are very important components of a high amylose breeding program, and can become a major cost factor in conducting an effective amylose development program.

Through the 1970s, only two types of high amylose hybrids were used in commercial production: Class V containing amylose percentages in the 50% range and Class VII which normally possesses from 70 to 80% amylose starch. Progress in amylose starch utilization has continued to generate interest for higher levels of amylose beyond the 70% range. Special breeding programs are necessary for the development of amylose inbreds having amylose values at the 70% level and above. Experience has shown that most breeding sources do not possess the assortment of modifier genes needed to reach these high amylose percentages. Therefore, some cyclic breeding system is needed to accumulate and select the favorable alleles involved in amylose starch synthesis prior to employing a regular inbred development program. In a presentation at the 1958 National Chemurgic Conference in Chicago, a participant implied that it would not be possible for corn breeders to develop breeding populations having amylose levels above the 80% level.[67] He also indicated that it would be necessary to discover at least one new gene for regulating amylose synthesis before amylose contents could be raised to 90% or higher. However, by 1958, Zuber et al.[43] had already broken the 80% amylose barrier. This report gave others the encouragement that even higher levels of amylose synthesis were attainable.

Early in the amylose development work, a form of recurrent selection seemed to be an acceptable breeding method for increasing the amylose levels in breeding populations; sub-

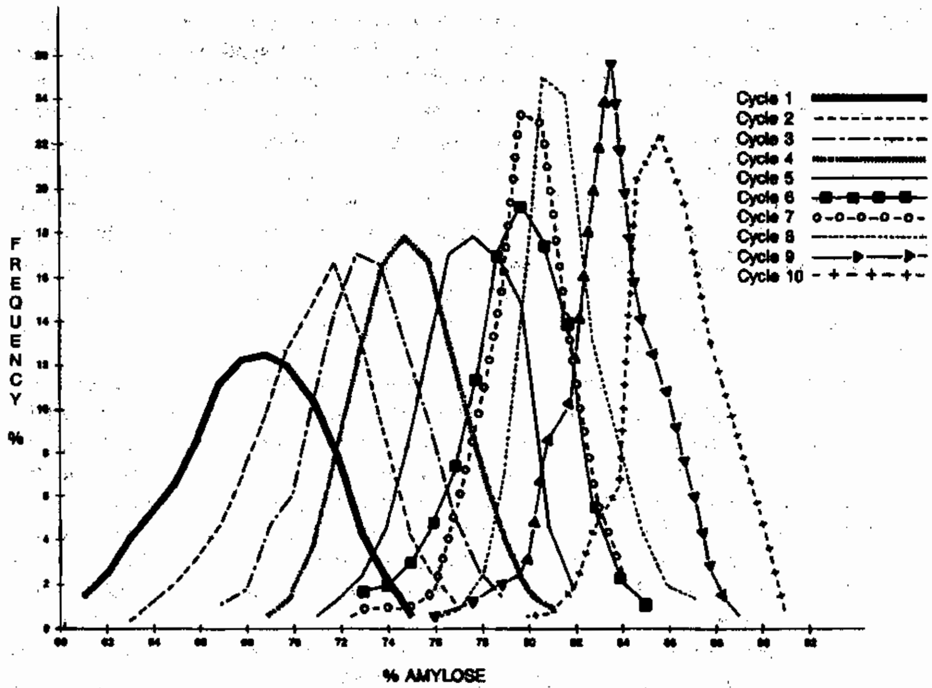

FIGURE 3. Progress from ten cycles of recurrent selection for increased amylose synthesis.

sequently, recurrent selection has become an integral part of the Custom Farm Seed Amylose Breeding Program. An example of the progress made after ten cycles of recurrent selection is shown in Figure 3. Additional selfing and selection within populations taken from this program resulted in breeding sources having in excess of 94% amylose starch. These selections were used as parents in additional breeding work for development of high amylose inbreds for use in Class VIII or Class IX hybrids. This type of program definitely requires a commitment to long-range breeding programs with a realization that very large sample numbers are required to have any reasonable assurance of success in developing Class VII, VIII, or IX amylose hybrids. To conduct a high amylose breeding program for the development of amylose inbreds in the Class V through Class IX category, it is reasonable to assume that several thousand starch analyses per breeding generation may be required. The larger numbers would be required for those programs having limited amylose converted germplasm from which to start a breeding program. In addition, the number of analyses required would be greater with breeding objectives designed for increasing the levels of amylose synthesis beyond the 70% level in various breeding populations.

In 1979, Custom Farm Seed, a division of National Starch and Chemical Company, purchased the specialty breeding program of Bear Hybrid Corn Company which included both the amylose and waxy germplasm breeding program. Since that time Custom Farm Seed has been the only seed company developing and marketing proprietary Class V, VI, and VII high amylose hybrids. These hybrids have been developed from germplasm utilizing the *ae* gene and associated modifiers.

In 1988, Stinard and Robertson,[68] described a dominant *amylose-extender* mutant (*Ae*-5180) that they discovered in a mutator population. They reported the phenotype expression of *Ae*-5180 in several germplasms as varying from "slightly shrunken and tarnished to

wrinkled sugary to brittle" regardless of whether it is present in the endosperm as one, two, or three doses. This mutation was placed on chromosome 5 and was shown to be a dominant allele of *ae* (amylose-extender). This dominant allele is fully female-transmissible but may have a reduced transmission through the male. They also reported the presence of maternal effects (similar to those found with the recessive *ae*) when crossing *Ae*-5180 sources by various dent and flint inbreds. For example, the inbred B73, when used as a female in crosses involving the *Ae*-5180 genotype, results in a glassy, near brittle phenotypic expression. The use of the dominant amylose extender gene in high amylose hybrid production presents some potential problems for maintaining purity of commercial grain. Foundation and commercial seed impurities would be areas of concern to the seed producer and would be more difficult to determine compared with those foundation and commercial lots produced from the recessive (*ae*) germplasm. A series of questions are yet to be answered in reference to the *Ae*-5180 allele, its implications in high-amylose breeding programs, and the subsequent use of high amylose hybrids from these development programs in the speciality starch industry. Perhaps history may eventually reveal that the discovery of the dominant amylose-extender allele did not have any significant impact on pre-existing amylose breeding programs.

C. PRODUCTION AND MANAGEMENT OF AMYLOMAIZE

Amylomaize grain production comprises a very small fraction of the total corn acreage in the U.S. It is normally produced only by farmers having contractual agreements with domestic wet milling companies or with exporters of specialty corn grain. Only two corn wet milling companies in the U.S. currently contract for and process high amylose grain. The National Starch and Chemical Company, with wet milling facilities at Indianapolis, IN, and Kansas City, MO, is the largest consumer of this specialty. The only other remaining U.S. wet miller still involved in the use of high amylose grain is the American Maize Products Co. Essentially 100% of the high amylose seed currently being used in the U.S. has been developed, produced, and marketed by Custom Farm Seed of Momence, IL. Two classes of amylomaize grain are currently being utilized by the wet millers: Class V hybrids producing grain containing approximately 55 to 60% amylose starch and Class VII hybrids having a 70 to 80% amylose starch content.

Amylomaize hybrids require special management and cultural requirements to provide more assurance of optimum grain production of acceptable quality and purity. High amylose seed has slower germination and subsequent emergence rates than normal dent types. Consequently, recommendations are made to the grain producer that amylose should not be planted in cool wet soils. Other than some reductions in planting rate, and having adequate field isolation for maintaining grain purity, the cultural requirements for amylomaize are similar to those recommended for normal dent corn production. Grain yield potential of high amylose hybrids is less than most commercially grown dent or waxy hybrids. Test plot results from Custom Farm Seed involving 5 years of replicated yield trials revealed yield differentials of 20 to 25% (Table 1) when amylomaize hybrids were compared with dent and waxy hybrids. It is not unusual for some grain producers to compare their best dent or best waxy hybrid yields with that of the average yield performance of their amylose hybrids. Using this criterion for comparison, larger differentials could occur. Realistically, however, performance should be based on all hybrids produced under comparable cultural and environmental conditions. Premiums are paid to the grain producer to compensate for yield differentials and special production, harvesting, and storage requirements.

Since high amylose starch synthesis is regulated primarily by a recessive gene (*ae*) and its modifiers, it is vital for the producer of amylomaize grain to adhere to specific production practices. Precautions should be taken to minimize the amount of foreign (non-amylomaize)

TABLE 1
Comparative Grain Yield Performance of Dent-Waxy with Amylose-Maize Hybrids

		Dent-waxy hybrids		High-amylose hybrids			
Number of locations[a]	Year	Average ($q\ ha^{-1}$)	High ($q\ ha^{-1}$)	Average ($q\ ha^{-1}$)	High ($q\ ha^{-1}$)	Average vs. average %	High vs. high %
3	1984	93	112	68	84	27	25
3	1985	95	114	75	90	21	21
2	1986	82	102	65	84	21	18
3	1987	96	116	79	92	18	21
2	1989	111	127	89	100	20	21
	Avg.	95	114	75	90	21	21

[a] All locations involve 48 hybrids in each category.

pollen contamination within the high amylose production fields. Planting amylomaize hybrids either too close to non-amylomaize fields or by planting amylomaize in fields having the potential of non-amylomaize volunteer plants could result in foreign pollen contamination and reduction in desired grain purity. Preventive measures must also be considered at harvest, drying, shelling, transportation, and storage to reduce the risk of non-amylomaize grain contamination and the subsequent rejection of putative amylomaize grain by the consumer or processor. Since the cost of amylose grain to the wet miller may be more than 50% higher than normal dent, it is imperative that the processor not only receive desired purity, but also that the grain must possess the necessary physical and chemical qualities. Improper artificial drying of high amylose grain can reduce the value to the processor. Therefore, strict guidelines for proper drying procedures must be rigidly followed by the grain producer to prevent deterioration of the milling and starch qualities of the high amylose grain.

Experienced farmer producers of amylomaize grain have learned that this enterprise can generate additional profits beyond their normal dent corn production program. The key to this success is recognizing the best cultural practices required for optimum amylomaize grain production and subsequent strict adherence to them. Since amylomaize grain garners a higher premium to the producer, it behooves him to maximize his profits through good management.

D. UTILIZATION OF HIGH AMYLOSE GRAIN

Space allocation for this chapter does not permit a complete or even an adequate review of the complexity of uses for amylose starch in various industries. Fortunately, however, references are available which are excellent compendiums covering a multitude of of applications for amylose starch.[3,69–77] Included in these references are examples for the use of this unique starch in the food, paper, textile, corrugating, and adhesive industries. Extensive applications for high amylose starch within each of these areas are expounded upon, thereby revealing the tremendous impact that amylose starch has had on the development of many consumer products. Young,[3] in an excellent review of the amylose starch, lists over 30 areas where amylose provides a significant function. This list is being expanded quite rapidly as new developments in amylose starch utilization are being discovered. As stated earlier in this chapter, the amylose component of starch possesses unique chemical and physical properties which result in specific functionalities. Usually some form of chemical or physical modification of the amylose starch molecule is required prior to its actual use in most industrial or food applications. These modifications enhance its functionality, thereby expanding its usefulness in various applications. For example, amylose starch when released into solution readily hydrogen bonds to form rigid opaque gels.[70] High amylose starch gels rapidly with subsequent formation of high strength gels which are useful in the confectionery

industry because some types of candy require a stabilizer to give shape and integrity to these candy pieces. By using amylose starch in making candy gum drops, the molding and curing time has been reduced at least sixfold or more, thereby resulting in lowering production costs as well as increasing the production capacity of the candy manufacturer.

Amylose starch serves other functions in the food industry, including its use as a thickener in various puddings and processed foods.[3] It can be used as a binding agent for preparing dehydrated potatoes or as a coating to reduce oil absorption of deep fat fried potatoes. Tomato paste and applesauce texture is enhanced by the addition of modified amylose starch.

Amylose starches are used extensively in the corrugating and adhesive industries as a carrier because of their resistance to shearing stresses, high film strength, and water resistance. Just a few years after the first commercial production of high amylose hybrids, amylose starch was reported as having film-forming properties similar to cellophane.[78,79] Subsequent research eventually led to the use of amylose starch in many types of films and packaging coatings.[3] Amylose films are characterized as having excellent transparency, flexibility, tensile strength, and water resistance.

Many other uses of amylose starch in various industrial and food applications are known, but perhaps the greatest break-through in the use of amylose starch has occurred recently.[80] An exhibit by the National Starch and Chemical Company at the 1990 Chicago Packaging Expo introduced a unique packing material made from Hylon VII® cornstarch. This loose fill packing referred to as ECO-FOAM™ visually resembles the polystyrene foam "plastic peanuts" widely used in the packaging industry. Polystyrene foams, however, have drawn criticism as a potential landfill problem due to both their bulky nature and bio-degradability resistance. ECO-FOAM is described by the National Starch and Chemical Company as environmentally friendly as it is composed of 95% amylose starch which is almost completely degraded within a very short time.

Feeding trials in animal nutrition research have shown that amylomaize grain had no advantage as an animal feed compared to waxy or normal dent corn grain.[81] This may be attributable to amylose starch being less digestible than the amylopectin starch fraction found in normal dent and waxy corns.[82] Similar inferences could be made from data reported by Peters et al.[83] and Fergason et al.[84] when Angoumois grain moths, (*Sitotroga cerealella* (Oliv.), were reared on high amylose corn grain. Larvae feeding on the high amylose kernels developed more slowly; subsequently, fewer moths reached the adult stage and weighed less than moths reared on normal dent corn. It was suggested that this insect could possibly be used to enhance selections for higher levels of amylose synthesis in a specially designed high amylose breeding project.[84] The data revealed nearly a 10% increase in amylose synthesis after seven cycles of recurrent selection when a heterogeneous composite sample of high amylose germplasm was exposed to the adult and larvae stages of the Angoumois grain moth.

New discoveries for the application of high amylose starch will continue to be found. Therefore, greater demand for high amylose grain will occur; however, the acreage devoted to high amylose grain production will probably remain relatively small compared with normal corn.

IV. WAXY CORN

A. INTRODUCTION

Variations in chemical and physical properties of corn endosperm are often identified by unique phenotypic expressions which are usually controlled by single recessive genetic factors. A corn selection found in China in the early 1900s was described as having an endosperm with a dull, waxy-like appearance.[85] This endosperm trait was subsequently

found to be controlled by a single recessive gene on chromosome 9 and was designated as *waxy* (*wx*). It has also been referred to as *Chinese waxy* (*wx-c*) due to its origin of discovery. Coe et al.,[86] in a review of "The Genetics of Corn", emphasized the uniqueness of this phenotype and described the waxy trait as having a marble-like opacity with a hardness similar to normal corn. The distinctiveness of the waxy phenotype is so vivid that it is easily identified visually in most corn germplasm backgrounds; however, the moisture content of the kernel must be 16% or lower before the waxy trait can be recognized visually. Corn endosperms that are homozygous for the *wx* gene produce only the branched starch component (amylopectin), and are devoid of the linear amylose fraction. Another unique characteristic of the waxy trait is its specific staining reaction when exposed to a dilute solution of iodine.[87] Amylopectin starch from homozygous waxy kernels forms an iodine-starch complex resulting in a reddish-brown stain. Alternatively, starch containing various levels of amylose or nonwaxy starch will stain blue to black when treated with potassium iodide. *Argentine waxy* (*wx-a*), an allele at the *wx* locus first reported by Andres and Basciollo,[88] is known to produce small amounts of amylose (< 5%) and gives an intermediate staining reaction with iodine. Other mutant alleles at the *Wx* locus have been reported which possess similar starch properties to those observed with *wx*.[89,90]

References to the biosynthesis of amylose and amylopectin starch have been made earlier in this chapter and will not be covered again in this section. Since this section is devoted to waxy corn, no attempt will be made to elucidate on the various genetic interactions involving the *wx* gene and other mutants located at other loci in the corn genome. Research has shown that the *wx* gene is epistatic to all known endosperm mutants, thus accounting for the absence of amylose starch when the *wx* gene is present.[91,92]

B. BREEDING WAXY CORN

From its introduction into the U.S. in 1909 and until the mid 1930s, the waxy gene was used primarily as a curiosity. Eventually, it came to be used universally as a marker in various genetic studies and experimental systems. By the early 1940s, work at the Iowa Agricultural Experiment Station revealed that the amylopectin starch from waxy corn had properties similar to tapioca starch obtained from roots of the cassava plant (*Manihot utilissima*).[93,94] Due to difficulties in importing tapioca from the Far East during World War II, the commercial production of waxy corn was begun. There was no apparent speculation at that time on the potential growth of this new specialty corn in either the U.S. or world markets. However, new discoveries for waxy starch applications over the last half-century has resulted in a substantial growth in acreage planted to waxy corn in the U.S., Canada, and Europe. This growth has been enhanced by the breeding efforts devoted to the continued improvement of waxy hybrids. Other than the original breeding program at the Iowa Agricultural Experimental Station, most of the waxy corn improvements have been made by corn breeders within the private sector of the seed corn industry. Presently, there are probably fewer than six private seed companies devoting any significant breeding efforts to the development of waxy corn hybrids.

Unlike the complexities associated with hybrid improvements of high amylose corn, waxy corn breeding programs are generally more conventional and less laborious. This phenomenon is due to the unique expressivity of the waxy gene in corn germplasm and the ease with which it can be transferred between and within breeding populations. Emphasis is again placed on the unique staining characteristics of the waxy trait within the endosperm when phenotypic expression of the waxy gene is masked by other factors such as high moisture levels or aleurone color. The *wx* trait may also be easily classified in pollen grains by staining with a dilute solution of potassium iodide.[95] Pollen grains having only amylopectin starch stain reddish-brown while the non-waxy pollen grains containing amylose starch will

stain dark blue to black. Heterozygous *Wxwx* plants should produce equal quantities of pollen grains of both genotypes. This pollen staining phenomenon makes it easier to select for the desired genotype in a breeding population prior to performing pollination procedures. This technique is especially helpful in a continuous backcrossing program designed to transfer the waxy gene in an inbred line-conversion program.

The breeding techniques or methodology a breeder might choose in any specific waxy development program is dependent upon many considerations including the breeding objectives, resources available, type of breeding populations or germplasm, level of expressivity of traits being selected, etc. The list of variables can be expanded considerably, but the breeder has to consider each program individually before choosing among the alternatives.

From the onset of many waxy inbred development programs, the backcross method has probably been the most popular. There is one compelling reason to choose this breeding method for waxy hybrid improvement. Competition among private seed companies to provide superior performing waxy hybrids as fast as possible encouraged many breeders to rely upon the relatively simple backcross breeding method. Consequently, conversion of elite dent lines used in the best commercial dent hybrids would provide the fastest and probably the most positive results. There are limitations, however, imposed by the backcross breeding approach. New hybrid developments would theoretically be expected only to equal but not to exceed the performance of their normal dent counterparts and would probably be inferior to newer, more current dent hybrid developments. This breeding procedure necessitates that the waxy corn breeder choose alternative breeding methods designed to circumvent some of the apparent limitations imposed by the backcross conversion method. Initially, most private waxy breeding programs did not have adequate reserves of waxy converted germplasms to permit their utilization of more complex waxy breeding schemes. More flexibility within these programs has ensued as a few private waxy breeding programs have been expanded to increase their array of available waxy breeding populations. These programs should have advanced to the stage where breeding procedures could be pursued that are similar to those in some of the more competitive dent corn breeding programs within the seed corn industry.

It is not the intent of the author of this section to outline a breeding program for waxy hybrid improvements. However, the obligation exists to emphasize that breeding procedures applicable to waxy corn are, with minor exceptions, similar to those used in normal dent corn programs. The major requirement is the presence of the waxy gene within the source breeding population at a frequency that would provide a reasonable level of success in recovery, assuming proper selection techniques were used. For example, in a pedigree-selection scheme performed within a breeding population derived from crossing two elite inbred sources, it is necessary that only one of the two inbred lines contribute the waxy gene to the population. This is the only additional genetic trait, compared with a normal dent breeding program, that has to be considered in the selection process. Adequate sample size of the source breeding populations is, however, of prime importance. Pollen staining of segregating or heterogeneous populations is a valuable technique in the selection phase of waxy inbred development programs. Hallauer et al.[96] implied that most applied corn breeders use similar procedures and perhaps similar germplasm sources in their dent inbred development programs. They also emphasized that minor variations between breeding programs exist including size of breeding populations, selection intensity, and subsequent testing procedures. Their discussions reveal the freedom that individual breeders have in choosing among many alternative procedures which they feel are most applicable to their own program, and those which may provide the greatest contribution to the success of their goals whether they be of short or long-term duration. The ultimate success of any well-designed program has been dependent upon the breeder's ability to select those progeny that will contribute in a positive direction toward the progress of the program.

TABLE 2
Relative Yield Performance of 5 Waxy Hybrids vs. Their 5 Dent Counterparts

Hybrid	Number of comparisons	Dent version Moisture (%)	Dent version Yield (q ha^{-1})	Waxy version Moisture (%)	Waxy version Yield (q ha^{-1})	Difference (yield) (%)
A	20	22.2	100.3	23.3	94.8	−5.8
B	14	21.7	95.0	24.0	95.5	+0.5
C	18	22.3	103.3	23.4	96.2	−7.4
D	20	19.0	99.6	20.7	94.7	−4.9
E	12	20.7	85.0	22.0	85.3	0.3
	Avg.	21.2	96.6	22.7	93.3	−3.5

Choice of germplasm must be the most critical for any corn breeding program. It is essential that selection of inbred lines to be crossed together for use in a pedigree selection scheme must complement each other for those attributes that contribute to desirable plant performance and grain yield. The choice of germplasm to be used in a breeding program is a decisive factor in determining the most logical breeding approach to be used. Normally a combination of some scheme for population improvements in conjunction with inbred line development should be a part of most successful breeding programs.

Population improvement of germplasm breeding sources by some method of recurrent selection is just as applicable to a waxy breeding program as it is in normal dent programs. Most recurrent selection schemes, however, may be designed for a relative long-term approach and would require greater inputs of resources before any returns can be expected from a marketing aspect. Economics of a breeding program and the potential benefits from it have to be determined before making the final decisions on what approach to pursue. Waxy corn is considered a specialty type corn and does not have the market potential of normal dent; consequently, not all private seed companies involved in marketing waxy corn can justify an extensive breeding program including substantial expenditures into population improvement per se. Reconsiderations, however, are warranted if a private seed company has sufficient sales potential in both the dent and waxy corn markets.

The development of waxy inbred lines by self pollination within crosses among elite germplasm sources followed by selection and testing is a common procedure in most waxy corn breeding programs of the U.S. As indicated earlier in this section, the development of elite waxy inbred lines by the backcross method has been very successful. Regardless of the breeding methods used, waxy breeding programs can be enhanced by the employment of the pollen staining technique. This technique improves the efficiency of a program by eliminating pollination of plants which do not carry the *wx* gene. This technique is more applicable to consecutive backcrossing programs designed to obtain the maximum cycles per year and eliminates the necessity in a continuous backcrossing program for using test-crosses to detect plants having the waxy gene.

Progress in some waxy breeding programs has apparently been successful as revealed by the relatively competitive yield performance of waxy hybrids compared to normal dent hybrids. Yield comparisons among Custom Farm Seed waxy hybrids and their normal dent hybrid counterparts indicate yield differentials of 5% or less between the two types of hybrids (Table 2). Theoretically, there should be no expected yield differentials between a waxy converted hybrid and its normal dent counterparts. There is evidence available which indicates that waxy hybrids produce grain having a higher test weight than the corresponding dent counterparts (Table 3). Higher test weights should enhance the relative performance of waxy

TABLE 3
Comparative Test Weights of 14 Waxy Hybrids and Their Normal 14 Dent Counterparts from 2 Locations in 1982

Grain type	Number of comparisons	Test weight* (kg/M)
Waxy	28	751
Normal dent	28	736

* Measurements on F2 grain samples stored for 1 year under comparable conditions.

corn hybrids. There may be exceptions to comparative yields between waxy and dent hybrids if the breeder has not been effective in progeny selection while pursuing the backcross breeding program.

Most seed corn companies do not have a waxy corn breeding program, or if they do, it is an apparently small and insignificant part of their total breeding efforts. Nevertheless, there are some private corn breeders that devote a concentrated and substantial part of their breeding efforts to the continued improvement of waxy corn. These efforts, hopefully, will assure the commercial waxy grain producer that waxy hybrids should remain competitive in performance with the best dent hybrids.

C. PRODUCTION AND MANAGEMENT OF WAXY CORN

Waxy corn production, like high amylose, is controlled by a single recessive gene; therefore, seed production and quality assurance procedures for maintaining genetic purity should be very strict. It is essential in foundation seed, commercial seed, and commercial grain production fields that adequate isolations are maintained to avoid cross contamination arising from foreign or nonwaxy pollen. Most seed corn companies that produce waxy hybrid seed have isolation requirements sufficient to prevent undesirable outcrossing to nonwaxy sources. They should also have specified tolerance limitations for seed purity standards. For example, the quality assurance program of Custom Farm Seed specifies that foundation waxy seed used for commercial seed production must be at least 99.5% pure waxy seed. That factor in conjunction with strict isolation permits Custom Farm Seed to label all commercially sold waxy hybrid seed as being at least 97% pure waxy. All seed fields are thoroughly and systematically sampled prior to harvest to assure the company of maintaining these standards. Any portion of a seed field that does not meet these rigid standards is not harvested for seed processing.

A majority of the commercially produced waxy grain is produced under contract to wet milling companies. The contract agreements, in addition to specifying certain grain quality standards, also have waxy purity requirements of the waxy grain. It is obvious why these strict standards must be adhered to in the corn wet milling industry. Variations in the amylopectin components could result in failures by the wet milling processor to meet specific standards of the processed starch. Premiums are paid to the waxy grain producer by the wet miller or the waxy grain exporter as compensation for the extra quality control procedures that must be followed. Other than the prior-mentioned quality assurance requirements for waxy grain production, similar cultural practices followed in normal dent grain production are adequate for managing waxy grain production. Responses to fertility applications, diseases, insects, environmental stresses, etc. theoretically should not differ between waxy

hybrids and their normal dent counterparts because no physical or chemical differences should exist between these putative isogenic counterparts except in the kernel. Sucrose is the sugar of transport, but it is not normally converted into starch until it is translocated to the corn endosperm.

Only a relative few seed corn companies produce or merchandise waxy hybrids. Acreage devoted to waxy corn production probably makes up less than 1% of the total corn acreage in the U.S. Only those companies having a large proportion of this market can economically justify being in the waxy seed business. Information available from advertisements and product literature from various seed corn companies reveals that at least a dozen of them offer waxy hybrids for retail sales. Most of these companies offer fewer than five waxy hybrids covering a very narrow range in relative maturity. An exception is Custom Farm Seed of Momence, IL, which is recognized in the seed corn industry as a company very extensively involved in specialty corn research and development. At the time of the writing of this chapter they offered 20 waxy hybrids ranging in relative maturity from 83 to 122 days.

Most of the waxy grain produced in the U.S. for industrial utilization is under contract to three wet millers: National Starch & Chemical Company, A. E. Staley Company, and American Maize Products. These companies normally contract directly with waxy grain producers to fulfill their requirements for specialty hybrid grain. The National Starch and Chemical Company, which is also a large consumer of high amylose grain, would be considered as the largest wet milling processor of specialty grain. Their affiliation with Custom Farm Seed has resulted in the only fully integrated combination of seed producer and consumer within the U.S.

In addition to waxy grain being produced in the U.S. for the wet milling industry, there is additional acreage of waxy grain grown for export and/or for use as feed in the livestock, dairy, and poultry industries.

D. UTILIZATION OF WAXY CORN

Wet milling of corn grain is a process used to separate starch from other constituents, such as fiber, germ, protein, and other minor extraneous materials.[1] The separation is enhanced by steeping or soaking grain in warm water containing sulfur dioxide. After the starch is separated from the other components, additional steps in the extraction of pure starch are required, including screening, washing, and eventually drying.[97]

The recovery of waxy starch is only the first step in a multitude of possible treatments or modifications that starch can be subjected to prior to its utilization in food or industrial applications. The unique properties of waxy cornstarch compared to normal dent corn is partially attributable to the absence of the amylose fraction present in dent corn. Additional properties such as degree of branching and length of side branching of the starch polymer also have an impact on determining uniqueness within waxy starches. The large size of the amylopectin molecule and its branched nature reduce the tendency for amylopectin polymers to form hydrogen bonding and subsequent retrogradation.

All plant starches are unique due to their specific chemical and physical properties. Most starches in their native or unmodified form have limited use in various industries. Therefore, most starches including waxy cornstarch are modified either to improve or repress their inherent properties as may be required for special use applications. For example, the general procedure of cross-linking waxy starches through the use of various chemical reagents improves the integrity of starch granules by reinforcing the hydrogen bonds in the granule, thus inhibiting swelling and eventual rupturing of the granule per se. Many types of modified waxy starches have a multitude of applications in the paper, textile, corrugating, and adhesive industries in addition to an enormous array of applications in the food industry.[1,69,70,72–77,98]

Modified waxy cornstarches serve essential functions in foods, including the improvement of uniformity, stability, and texture in various food products. The apparent benefits from these functions include the improvement of smoothness and creaminess in canned foods and dairy products, better freeze-thaw stability in frozen foods, and more desirable texture and appearance in dry foods and mixes.

Major advancements in papermaking technology are in part related to the availability of new types of modified waxy starches. These starches essentially provide binding or bonding qualities to the papermaking process, as well as adding other essential features, including improved sizing for greater paper strength and printing properties. Papermaking is a very complex and highly technical science which cannot be adequately covered in the space allocated to this chapter. Progress in papermaking technology is occurring rapidly and is therefore adding substantially to the wealth of information previously available.

Waxy cornstarches also are used in various textile finishing processes because of their clear film forming properties.[74] The unique properties of waxy cornstarch provide for additional application in the textile, corrugating, and adhesive industires.[69,72,77] Waxy cornstarch is a major starch component in adhesives used in making bottle labels. This waxy starch based adhesive imparts resolubilizing resistance to the labels which prevents their soaking off the bottle if immersed in water or being subjected to very high humidity conditions. In addition, waxy cornstarches are commonly used in the manufacture of gummed tapes and envelope adhesives.

An alternative to the use of waxy starch in various industrial and food applications is the use of waxy corn grain as livestock feed, which began to emerge in the 1940s. The use of corn in the feed industry has always held a lofty position because of its value in producing meat, milk, and eggs. Beginning with a research report in 1944, waxy corn seemed to have the potential to increase feed conversion efficiencies.[99] Additional feeding trials involving swine, beef and dairy cattle, lambs, and poultry were designed to compare the feeding value of waxy to normal dent grain.[81,100–102] Generally, the trials indicated an advantage for feeding waxy grain. Seldom have the investigations shown any negative or adverse effects from feeding waxy grain. Testimonials that indicate increases of both milk production and butterfat content are not uncommon when waxy corn is fed to lactating dairy cattle. Increases of more than 20% in average daily weight gains in fattening lambs were observed when waxy grain was compared with normal dent.[102] In addition, a 14.3% increase in feed efficiency was noted in favor of waxy grain. Likewise, an increase in feed efficiency approaching 10% was obtained in trials where waxy grain was compared with the dent counterparts when fed to finishing beef cattle.[102] Lower back fat and higher carcass grades have been reported in swine-feeding experiments (unpublished testimonials). As a result of the generally favorable advantages associated with feeding waxy grain, many livestock producers and dairymen use waxy corn as a replacement for normal dent in animal diets. Increased digestibility of the waxy starch may explain these advantages attributable to the use of waxy corn as a feed. Conversely, amylose starch present in normal dent corn has been suggested as being less digestible in studies performed on monogastric animals.[82] Since the amylose starch component is absent in waxy corn, this may add credence to evidence that waxy corn has been shown to be superior in animal diets.

Though the history pertaining to waxy corn and to its utilization is relatively brief, the cornstarch industry can be assured that the demands for this unique polymer will continue to expand, but at an unknown rate. World population growth, changes in modern living styles, the desire for more human conveniences, and progress in various industrial and food technologies will surely lead to greater demands on specialty polymers including waxy and amylose types.

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